Hydrobiologia (2009) 616:193–215
DOI 10.1007/s10750-008-9591-x

JELLYFISH BLOOMS

# A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation

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Published online: 11 November 2008
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**Abstract** Mass occurrence—aggregation, blooming, or swarming—is a remarkable feature of a subset of usually diverse scyphozoan clades, suggesting it is evolutionarily beneficial. If so, it should be associated with one or more phenotypic characteristics that are advantageous and which facilitate occurrence *en masse*. Here, we examine the evolution of morphological, ecological, and life history characteristics of medusozoans, focusing on the taxa that occur *en masse*. By tracing the evolution of aggregating, blooming, and swarming phenotypes, organismal traits, and environmental settings on an up-to-date synoptic phylogeny of classes and orders of Medusozoa, we are able to hypothesize circumstances that enable taxa to occur *en masse*. These include character states and character complexes related to podocyst formation, strobilation, oral arms, large size, and shallow-water habitat. These evolutionarily advantageous traits may be adaptations that evolved in response to selection for individual traits such as survival during periods of few resources, feeding on pulsed resources, and fecundity. These adaptations were apparently subsequently coopted by selection for reproductive success which favored mass occurrence. By considering the distribution of traits describing other phylogenetic lineages—when appropriately detailed ecological and systematic descriptions become available—it may be possible to predict which species are evolutionarily predisposed to form problematic blooms if environmental conditions permit.

**Keywords** Ecology · Evolution · Environment · Morphology · Phylogeny · Phenotype · Scyphozoa

Guest editors: K. A. Pitt & J. E. Purcell
Jellyfish Blooms: Causes, Consequences, and Recent Advances

**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-008-9591-x) contains supplementary material, which is available to authorized users.

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## Introduction

Large accumulations of jellyfish—aggregations, blooms, and swarms—are natural phenomena that apparently occur unpredictably spatially and temporally. Yet, taxonomically and phylogenetically, there are systematic patterns to their occurrence suggesting a certain suite of characteristics may predispose some medusozoans to occur *en masse* (Hamner & Dawson, 2008). If true, this would suggest that, assuming

relatively consistent phenotype-environment interactions, mass occurrences of jellyfish should be predictable.

The physical mechanisms that generate temporary aggregations of medusae have been reviewed (Arai, 1992, 1997; Graham et al., 2001; Purcell, 2005; see also Decker et al., 2007) and environmental correlations with blooming proposed for eutrophication (Arai, 2001), overfishing (Mills, 2001; Brodeur et al., 2002), and species introductions (Graham et al., 2003; Holland et al., 2004; see also Purcell et al., 2007). Specific organismal traits that relate to mass occurrence, though, have received less attention. Our goal here is to begin to assess whether certain organismal traits may be associated with accumulation.

To explore this proposition, we first examine morphological, ecological, and life-history characters in an explicitly phylogenetic framework. By plotting attributes of extant taxa on a phylogeny it is possible to trace back in time, into ancestral chronospecies (see glossary of terms in Electronic Supplementary Material, Appendix A), the likely (i.e., most parsimonious) origin and routes of inheritance of phenotypic characters. Phenotypic character states that apparently evolved at similar times may be causally related. To further examine the postulate that scyphozoan accumulations are evolutionary adaptations to planktonic life (Hamner & Dawson, 2008), we take two additional steps in this study. The second step is to identify possible adaptive benefits with respect to mass occurrence. The third step is to assess the relative chronology of their evolution and thus distinguish adaptations from exaptations. This permits us, finally, to consider whether the observation that "species that have always been present suddenly experience severe increases of 'blooms', often with little evidence of what caused the population increase" (Mills, 2001) may in fact be evidence that jellyfish blooms are exaptations to the currently rapidly changing world.

## Materials and methods

To infer the evolution of aggregating, blooming, and swarming within Scyphozoa, we used MacClade v.4.08 (Maddison & Maddison, 1989) to trace the states of these characters (Hamner & Dawson, 2008) on a phylogeny of medusozoans, emphasizing scyphozoans, that is consistent with the weight of evidence from molecular phylogenetic, morphologic phylogenetic, and morphologic taxonomic hypotheses (see Hamner & Dawson, 2008; also, e.g., Stiasny, 1921; Kramp, 1961; Collins, 2002; Dawson, 2004; Collins et al., 2006; Daryanabard & Dawson, 2008). The phylogeny in Fig. 1 was created by writing Newick format trees to describe well-supported subtrees in phylogenies published in the peer-reviewed literature, redrawing graphical representations of these Newick trees as cladograms in FigTree v.1.1.1 (A. Rambaut, 2007: http://www.tree.bio.ed.ac.uk/software/figtree/), and then using an Adams consensus or supertree type approach to splice together the graphical subtrees in Adobe Photoshop CS3 v.10.0.1; this composite consensus tree was rewritten in Newick format and imported into MacClade v.4.08. The seven hierarchically integrated Newick format subtrees drawn from published results were as follows: ((Staurozoa1,Staurozoa2),((Hydrozoa1,Hydrozoa2),(Cubozoa1,Cubozoa2),((Coronatae1,Coronatae2),(Semaeostomeae1,(Semaeostomeae2,Rhizostomeae)))))) from analyses of 18S rDNA by Hamner & Dawson (2008; see also Collins, 2002, Fig. 3). ((Coronatae1,Coronatae2),((Rhizostomeae1,Rhizostomeae2,Ulmaridae1,Ulmaridae2),Cyaneidae,Pelagiidae)) from analyses of 28S rDNA by Hamner & Dawson (2008; see also Collins et al., 2006, Fig. 3). ((((Mastigiidae,Thysanostomatidae),Cassiopeidae),Cepheidae),((Rhizostomatidae,Stomolophidae),Catostylidae)) from analyses of concatenated 18S, 28S, and COI by Hamner & Dawson (2008). (Atollidae,Atorellidae,Linuchidae,Nausithoidae,Paraphyllinidae,Periphyllidae) and (Cepheidae,(Mastigiidae,Versurigidae,Thysanostomatidae),Cassiopeidae) and ((Rhizostomatidae,Stomolphidae),(Lychnorhizidae,Lobonematidae,Catostylidae)) from Kramp (1961; see also Stiasny, 1921). (Other_Hydrozoa,(Other_leptothecates,Aequoreidae)) from Collins (2002; see also Collins et al., 2006). We also traced the evolution of canal structure, strobilation type, and photosynthesis across this consensus supertree. The coding of character states in extant taxa is shown by the boxes between branches and taxon names in the reconstructed phylogenies in Figs. 1 and 3.

To infer the evolution of morphological, ecological, and life-history characters possibly correlated with aggregating, blooming, and swarming in scyphozoans, we used MacClade v.4.08 (Maddison & Maddison, 1989) to trace the evolution of character

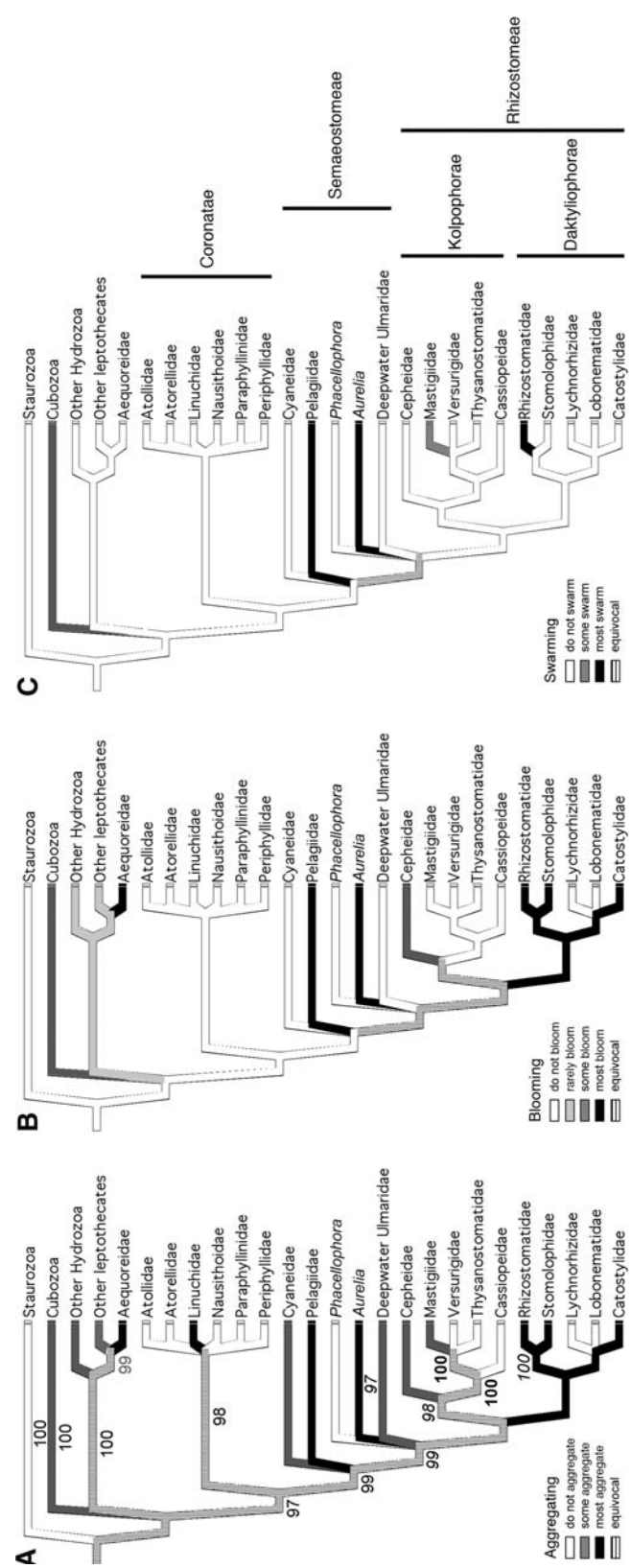



**Fig. 1** The phylogenetic distribution of the (**A**) aggregating, (**B**) blooming, and (**C**) swarming phenotypes in Medusozoa. Hypothetically, these phenotypes result from interactions among multiple component traits, ranging from largely environmental [aggregating], through largely life history [blooming], to largely organismal [swarming]. The 'supertree' is ultrametric, a consensus of the phylogenetically nested molecular analyses of Hamner & Dawson (2008), morphologic taxonomy of Kramp (1961), and molecular analyses of Collins (2002) and Collins et al. (2006). Bootstrap values, shown only in (**A**), are taken from the source phylogenies (gray, Collins (2002); black roman, 18S rDNA in Hamner & Dawson (2008); black italic, 28S rDNA in Hamner & Dawson (2008); black bold, concatenated 18S, 28S, and COI analyses in Hamner & Dawson (2008)) and thus indicate support for branches in the component subtrees, as annotated. Aggregations are defined as an accumulation of individuals that consequently likely interact. Blooms are restricted to 'true' blooms which are defined as normally and abnormally abundant seasonal appearance of jellyfish directly attributable to population growth. Swarms are defined as dense aggregations due to behavior. These three levels of accumulation are classified here as distinct character states for simplicity in our initial analyses, but may be artificially discrete classifications of a character complex whose states are continuously distributed. Small blocks between terminal branches and taxon names indicate how the character state was coded for that taxon; no block indicates coded as unknown and, therefore, any state indicated by the branch color is inferred rather than observed. Ancestral character states about which phylogenetic inference is ambiguous are shown as 'equivocal'

states coded in the datamatrix of van Iten et al. (2006). Although Marques & Collins (2004) and van Iten et al. (2006) have previously used parsimony analyses to infer phylogeny and patterns of evolution of anatomical, morphological, and life-history traits across classes and orders of medusae, such analyses can be compromised by homoplasy and tautology because phylogeny is reconstructed using the same characters whose pattern of evolution is then inferred from the phylogeny (Armbruster, 1992). These problems have been much debated (e.g., de Queiroz, 1996; Luckow & Bruneau, 1997), and may not substantially affect results if the true phylogenetic signal is strong or if particular methods are used (e.g., Ronquist, 2004), but cladistic approaches are compromised when the shape of the phylogeny is sensitive to inclusion or exclusion of the evolutionary hypothesis or characters (Zrzavy, 1997; Brooks & McClennan, 2002, p. 58). The results of Marques & Collins (2004) and van Iten et al. (2006), which differ greatly in topology due to re-weighting of a subset of characters, suffer from at least the latter. Thus, we reanalyzed the phenotypic data using a constraint cladogram derived from the molecular analyses of Collins et al. (2006; see also analyses of 18S rDNA and 28S rDNA by Hamner & Dawson, 2008), as follows: (Staurozoa,(Hydrozoa,(Cubozoa,(Coronatae,(Semaeostomeae,(Rhizostomeae))))))).

**Fig. 2** Schematic of the phylogeny of Tesserazoa (i.e., non-anthozoan cnidarians) on which are plotted the evolution of mass occurrences and characters potentially correlated or causally related to aggregating, blooming, and swarming. The phylogenetic relationships are constrained to conform to those indicated by recent molecular analyses (e.g., Collins et al., 2006; Hamner & Dawson, 2008). The evolution of 87 characters documented by Van Iten et al. (2006; modified from Marques & Collins, 2004) were traced on the tree, and branch lengths are proportional to the numbers of unambiguous character changes (minimum tree length = 79 steps, for reference the branch to Staurozoa is four steps). Only characters synapomorphic for (i.e., shared by members of a clade, but not their most recent common ancestor) the clades Cubozoa + Scyphozoa, Scyphozoa, Discomedusae, or Rhizostomeae are plotted in the figure. Directionality of character evolution within Medusozoa is polarized by rooting the phylogeny using outgroups Anthozoa (not shown) and Staurozoa. The relative timing and direction of evolutionary transitions are then indicated by branches annotated as follows "Character: ancestral state ⇒ derived state." The non-homoplastic synapomorphies (□) represent the key evolutionary transitions associated with evolution of occurrence *en masse*. Also shown are homoplasious character state changes (◇, ▽, Δ) which are unlikely to have a large impact on the ability of the species to occur *en masse* because they also occur in clades that do not bloom. The approximate proportions of families with aggregating [A], blooming [B], or swarming [S] species were estimated from Hamner & Dawson (2008) and are indicated by the pie charts embedded within the tree. The state of mesoglea (non-cellular ⇒ cellular) is homoplasious with the character state in Anthozoa; heterotrichous anisorhizas are coded polymorphic for the clade Anthothecata + Siphonophorae (van Iten et al., 2006); strobilation is coded as fixed for monodisc strobilation in all Rhizostomeae following van Iten et al. (2006) although this is the case only for Kolpophorae (see Fig. 3A)

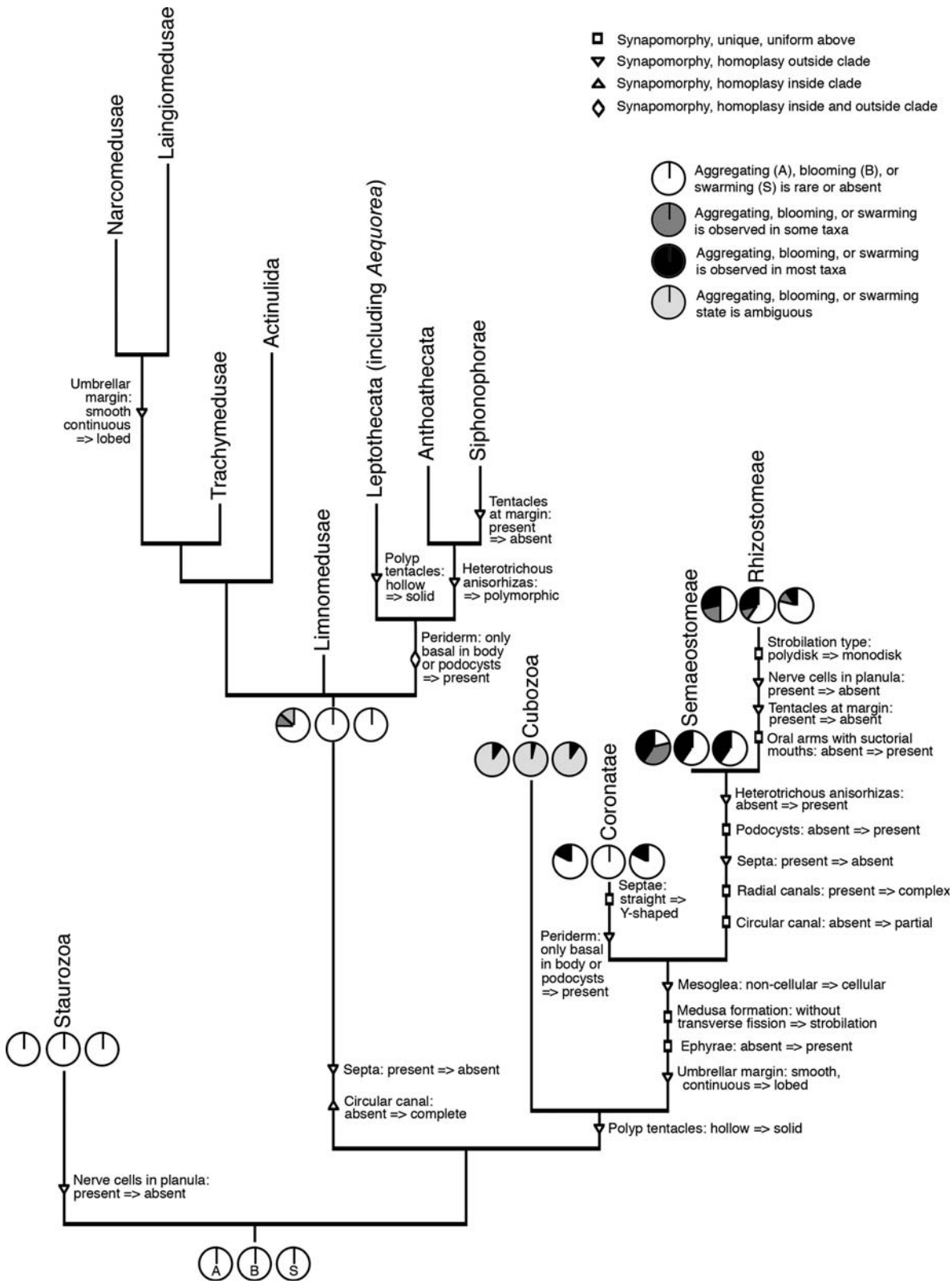
## Results

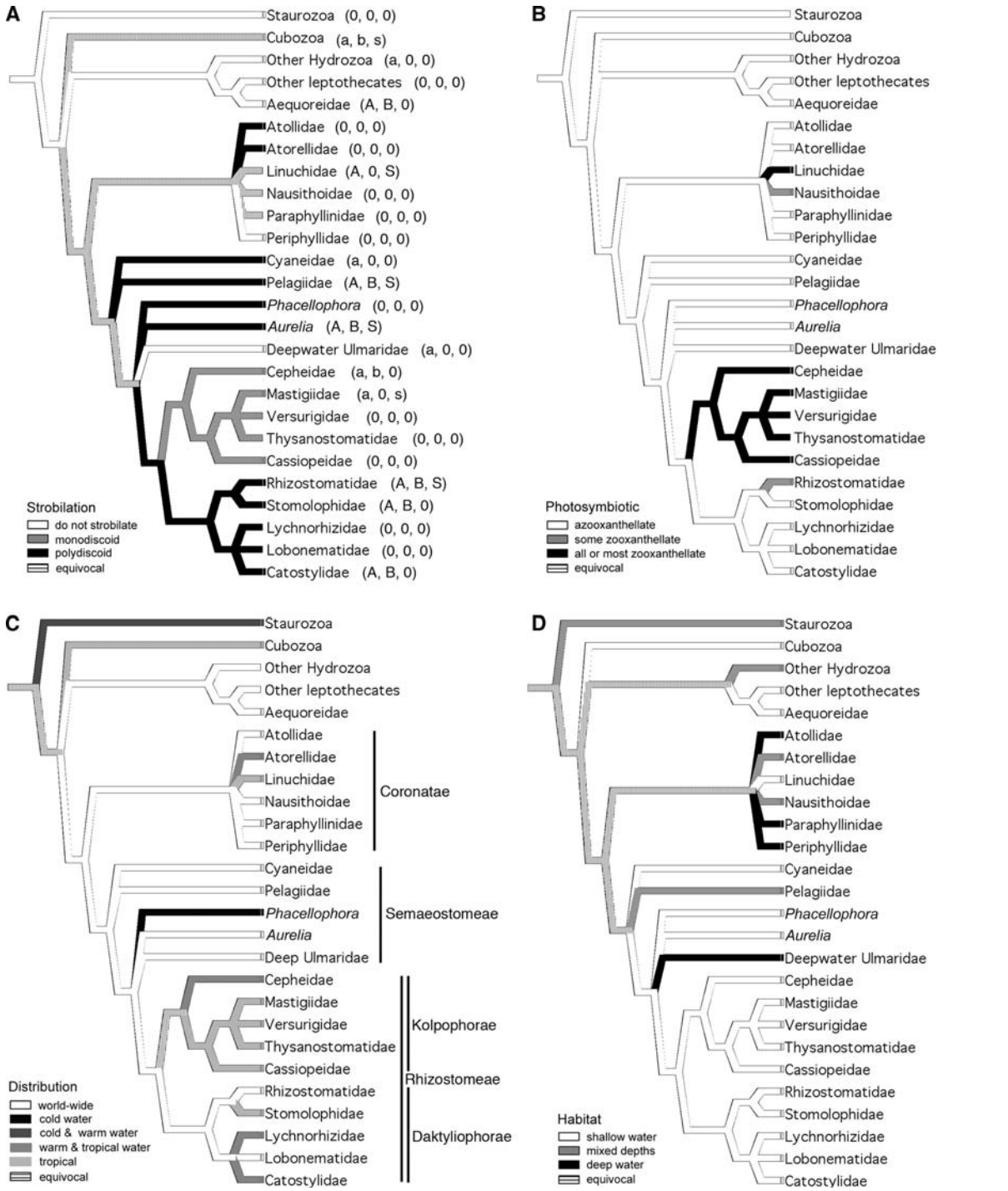
Mass occurrences of medusae are not distributed evenly phylogenetically. Although species that aggregate can be found in all medusozoan classes, species that bloom or swarm are restricted almost entirely to Class Cubozoa and to Subclass Discomedusae within Class Scyphozoa (Fig. 1). Evolution of aggregations appears to precede evolution of blooms and/or swarms.

Considering the evolution of morphology and life history, we found up to 13 'synapomorphic' characteristics of Scyphozoa potentially related to their ability to form blooms and swarms (Fig. 2). Of these, only seven were unique synapomorphies for Scyphozoa or a subclade thereof in our ordinal-level analysis (Fig. 2): podocysts (can be formed), strobilation (absent, present), strobilation type (monodisc, polydisc), ephyral life-history stage (present), circular canal (present either partially or complete), radial canals (present, complex), and oral arms (with suctorial mouths). Other life-history, ecological, and distributional attributes of extant medusae are also clustered in more basal or more derived taxa (Fig. 3). Circulatory canals, for example, originate in Cyaneidae and tend to be more complexly anastomosing in more highly derived taxa (Ulmaridae and particularly Rhizostomeae; Fig. 4).

## Discussion

Aggregation, which is widespread in Medusozoa, is apparently an evolutionarily basal trait and a precursor to the blooming and/or swarming phenotypes which most often characterize cubozoans and scyphozoans (Fig. 1; see also Dawson & Hamner, 2008). The implied evolutionary trajectory is intuitively appealing. It is easy to conceive that selection for


Synapomorphy, unique, uniform above
Synapomorphy, homoplasy outside clade
Synapomorphy, homoplasy inside clade
Synapomorphy, homoplasy inside and outside clade
Aggregating (A), blooming (B), or swarming (S) is rare or absent
Aggregating, blooming, or swarming is observed in some taxa
Aggregating, blooming, or swarming is observed in most taxa
Aggregating, blooming, or swarming state is ambiguous
Narcomedusae
Laingiomedusae
Trachymedusae
Actinulida
Leptothecata (including Aequorea)
Anthoathecata
Siphonophorae
Limnomedusae
Cubozoa
Coronatae
Semaeostomeae
Rhizostomeae
Staurozoa
Umbrellar margin: smooth continuous => lobed
Tentacles at margin: present => absent
Polyp tentacles: hollow => solid
Heterotrichous anisorhizas: => polymorphic
Periderm: only basal in body or podocysts => present
Septa: present => absent
Circular canal: absent => complete
Nerve cells in planula: present => absent
Polyp tentacles: hollow => solid
Septae: straight => Y-shaped
Periderm: only basal in body or podocysts => present
Strobilation type: polydisk => monodisk
Nerve cells in planula: present => absent
Tentacles at margin: present => absent
Oral arms with suctorial mouths: absent => present
Heterotrichous anisorhizas: absent => present
Podocysts: absent => present
Septa: present => absent
Radial canals: present => complex
Circular canal: absent => partial
Mesoglea: non-cellular => cellular
Medusa formation: without transverse fission => strobilation
Ephyrae: absent => present
Umbrellar margin: smooth, continuous => lobed
A
B
S




traits favoring aggregation, a phenomenon caused primarily by environmental characteristics exaggerated by directional swimming elicited in response to the immediate environment, is possible in many diverse taxa including ancestral medusozoans that likely were as anatomically complex as modern-day medusozoans (Cartwright et al., 2007). Such changes anticipate benefits of accumulation that could increase as a consequence of either further selection on newly evolved adaptations or new selection on

◀**Figure 3** Characteristics of organisms and environment that may affect the occurrence of aggregations, blooms, or swarms. (**A**) Strobilation; note that this rendition codes asexual reproduction of cubomedusae from polyps as a form of strobilation, following Straehler-Pohl & Jarms (2005), although following Werner (1973) the branch leading to Cubozoa would be colorless, indicating 'do not strobilate.' (**B**) Whether medusae are photosymbiotic or not. (**C**) The predominant geographic, i.e., latitudinal and longitudinal extent, distribution of medusae. (**D**) The predominant depth zone, or zones, of occurrence of medusae. Small blocks between terminal branches and taxon names indicate how the character state was coded for that taxon; no block indicates coded as unknown and, therefore, any state indicated by the branch color is inferred rather than observed. States about which phylogenetic inference was ambiguous are shown as 'equivocal.' Letters after taxa in (A) indicate whether some/most aggregate 'a/A,' bloom 'b/B,' or swarm 's/S,' a '0' indicates none show that kind of accumulation. Higher taxonomy is indicated in (C) for convenient reference

exaptations (i.e., other traits, evolved previously, that acquired new evolutionary value in the novel context of aggregations) leading to evolution of blooming and/or swarming. Concomitantly, the most complex aggregative behavior, swarming, is observed in the fewest taxa. This indicates that accumulation likely results from interactions among multiple characters, rather than being a consequence of single 'Mendelian' traits. Accumulation therefore may be modified by natural selection either on component characters or on the complex behavior as a whole.

Our molecular maximum likelihood phylogeny (Hamner & Dawson, 2008), like the morphological parsimony analysis of van Iten et al. (2006) but in contrast to Marques & Collins (2004), places Staurozoa basal to Medusozoa rather than as a derived clade within Medusozoa. This apparently major rearrangement of phylogeny does not affect inference of the evolution of the states of, or phenotypes that may favor, accumulation of jellyfish for three reasons: (1) few characters unambiguously distinguish Staurozoa from Medusozoa, (2) the relationships of Scyphozoa to putative sister taxa, Cubozoa or perhaps Hydrozoa, are not altered, and (3) the relationships within Scyphozoa are not altered. Thus, in addition to the giant fiber nerve net and statocysts characteristic of pelagic motile medusae (Marques & Collins, 2004) which can aggregate, 13 'synapomorphic' characteristics of Scyphozoa are potentially related to their ability to form blooms and swarms (Fig. 2; see also Marques & Collins, 2004; Collins et al., 2006; van Iten et al., 2006) but only seven unique synapomorphies for Scyphozoa or a subclade thereof are indicated to be the characters [and states] that promote blooms and/or swarms. Below, we discuss these characters and states (listed in *Results*), in some cases grouping them into likely character complexes (e.g., circular and radial canals are both components of the gastrovascular canal system) and in others expanding the list to include related characters (e.g., tentacles, the canal system necessitated by large size, and large size which enables improved swimming ability) reconstructed ambiguously by, or not in the matrices of, Marques & Collins (2004) or van Iten et al. (2006).

## Podocyst formation

Podocyst formation is documented in all semaeostome families and in the rhizostome families Rhizostomatidae and Stomolophidae (Arai, 1997, p. 164). Podocyst formation is therefore also probably a life-history strategy conserved in other rhizostomes not yet studied in this regard.

Podocysts are small aggregations of epidermal cells and amoebocytes surrounded by a chitinous cuticle. They are formed in several ways, and one or many may be produced by a single scyphistoma. They have low metabolic rates and may have exceptional longevity; those of *Chrysaora quinquecirrha* (Desor) can be viable for 2 years or more (Arai, 1997, p. 164). On excystment, each forms a new scyphistoma. Podocysts may, therefore, contribute to blooms in two ways. One, by allowing populations to resist long harsh conditions that would decimate polyp or medusa populations and, when conditions improve, metamorphosing into scyphistoma that may produce many medusae. Two, by leading, as the products of asexual reproduction, to increased scyphistoma population size and therefore, via strobilation, potentially also to increased medusa population size.

## Strobilation, strobilation type, and ephyral life-history stage

Although metamorphosis of cubozoan polyps into cubomedusae may be a modified form of strobilation (Straehler-Pohl & Jarms, 2005), strobilation and the concomitant production of ephyrae is unequivocally present only in Scyphozoa. Within Scyphozoa, the

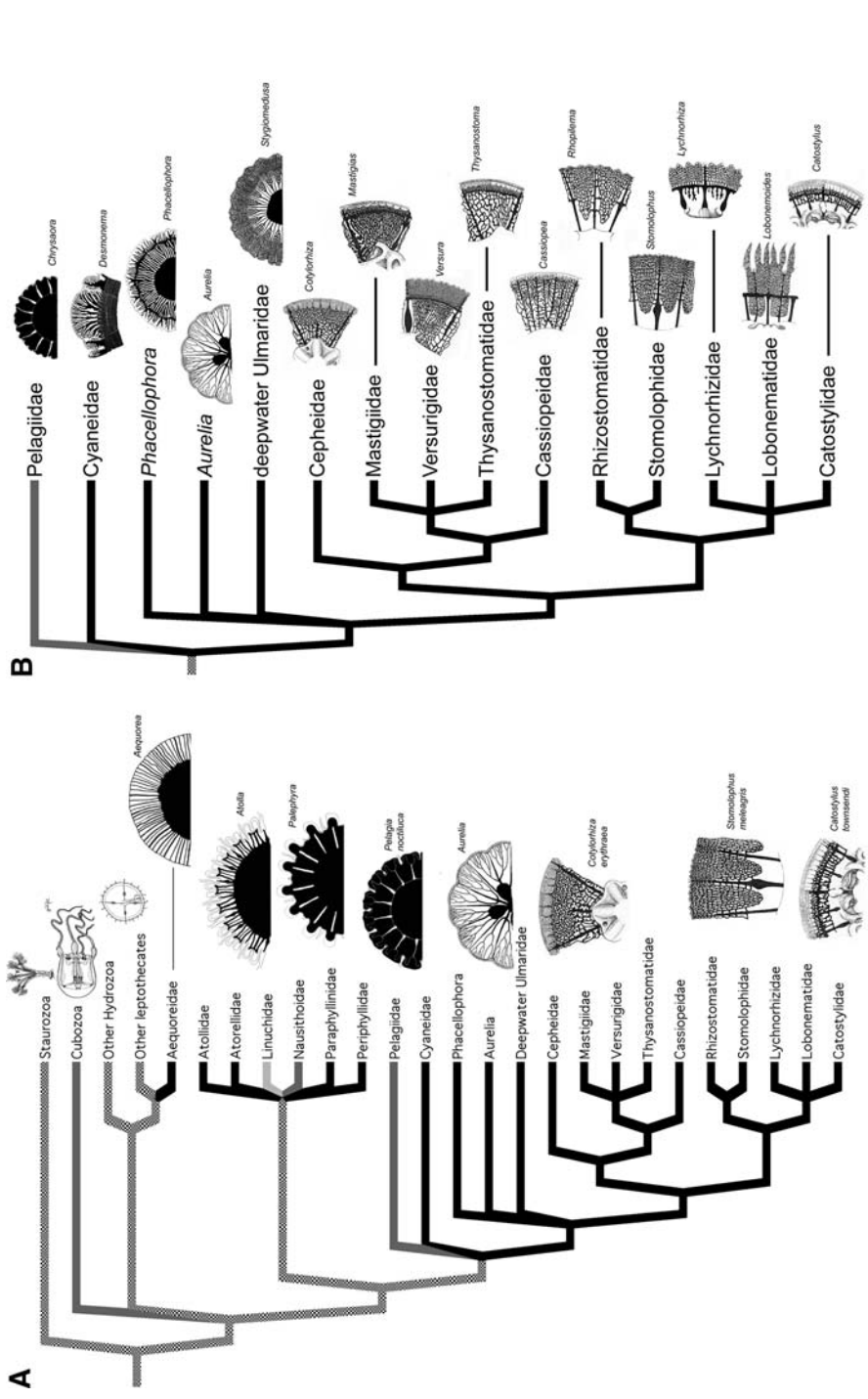



**Fig. 4** Evolution of size and canal structure in medusae: (**A**) general patterns across the Medusozoa and (**B**) more detail showing family-level variation within Discomedusae. Shading of branches in the trees indicates patterns of size evolution of medusa: light gray, predominantly small medusae; dark gray, mixed sizes of medusae; black, predominantly large medusae; hatched, phylogenetic inference of size is ambiguous. Illustrations of canal complexity are redrawn from Stiasny (1921), Kramp (1961), Larson (1986), Bouillon (1999), BIODIDAC (http://www.biodidac.bio.uottawa.ca/; image by Ivy Livingstone: Animalia—Cnidara—Cubozoa), and http://www.hermes.mbl.edu/BiologicalBulletin/KEYS/INVERTS/3/img/H.auricula1.JPG

biphasic life history and therefore strobilation and ephyrae predominate, with exceptions restricted to a single neritic species *Pelagia noctiluca* (Forskål) and a polyphyletic group of deepwater medusae (Fig. 3A), which have direct development (Larson, 1986; Jarms et al., 2002).

Almost all species that occur *en masse* do strobilate, whereas most species that do not occur *en masse* do not strobilate, suggesting that strobilation (or a correlated factor) does predispose jellyfish to occur *en masse*. However, *Pelagia noctiluca*, which is renowned for mass occurrence, develops directly from planula to ephyra (Rottini Sandrini & Avian, 1983) demonstrating that the polyp stage and strobilation are not necessary for bloom formation (a metagenetic life cycle is also not present in ctenophores or planktonic chordates which do form blooms).

Which species bloom may furthermore be influenced by the type of strobilation. Families in the rhizostome suborder Kolpophorae have monodisc strobilation (Holst et al., 2007) and rarely bloom or swarm (Fig. 1). In contrast, *Aurelia* spp., *Chrysaora* spp., and Rhizostomatidae all have polydisc strobilation and are the most notable blooming species. We hypothesize that the apparent association between polydisc strobilation and blooms is because polydisc strobilation probably produces more ephyrae per polyp per unit time, or more ephyrae per polyp at a particular time, than monodisc strobilation. However, Watanabe & Ishii (2001) may describe the only attempt to measure polyp productivity in relationship to strobilation, which means quantitative comparisons are not yet possible.

Whether strobilation, be it monodisc or polydisc, is itself a major factor contributing to blooms also depends on the number of medusae produced being impacted less by other processes, such as asexual reproduction via podocysts, planuloids, the preceding year's medusa population size and individual fecundity, or the survival of ephyrae. Yet, it is intuitive that simultaneous strobilation, particularly polydisc strobilation, could generate large cohorts of ephyrae leading to blooms of adult medusae.

## Canal system, medusa size, and dependent attributes

In stauromedusae and scyphistomae, the gastric system is divided in the suboral reaches by four septa along which run ciliary currents that distribute food and reverse to remove waste. Similar simple circulatory systems can be found in Cubozoa (e.g., Hamner et al., 1995) and Coronatae (Fig. 4). The gastric system is relatively simple in the phylogenetically basal scyphomedusae such as Pelagiidae and Cyaneidae in which septa completely subdivide the gastric cavity of the medusa into numerous pouches through which cilia move nutriment and wastes. In Cyaneidae, the pouches may additionally have distal canal-like protrusions and, in *capillata*-group medusae, pit-like intrusions into the deeply pleated subumbrellar circular and radial musculature (Stiasny & van der Maaden, 1943).

It is only in Ulmaridae and Rhizostomeae that the gastric system consists of a complex network of canals. In the basal *Phacellophora*, the system consists largely of multitudinous septae which create a complex pattern of radiating canals (see Figs. 2, 4). The remaining ulmarids have complex anastomosing networks of canals permeating the subumbrella. In *Aurelia* (Russell, 1970; reviewed by Arai, 1997, p. 100), the flow of food particles and waste is unidirectional except through the largest canals or through the mouth where ciliary currents are driven in opposite direction at different positions within the same tube. Little is known of the flow through the gastrovascular systems of other ulmarids or rhizostomes, but the complexly anastomosing canals of rhizostomes, particularly the dense meshes in Kolpophorae, appear at first glance to be likely to cause inefficient flow. We suggest, though, that directional flow through canals will be discovered when circulation is more carefully examined in all large medusae because efficient internal flows are required to regularly and completely flush the canals and to provide food and oxygen to densely packed and often folded tissues. All large organisms have mass-transport or circulatory system that move resources to, or waste products from, sites of origin to distant parts of the organism (Ruppert & Carle, 1983). The most relevant comparison is *Aequorea*, the largest hydromedusan, which has radial canals and ciliarly-driven flow (Hyman, 1940; Arai & Chan, 1989) evolutionarily analogous to the canals and flows in Ulmaridae and Rhizostomeae.

In terms of blooms and swarms, the importance of gastrovascular canals is perhaps not so immediately obvious as that of the rate of podocyst formation or

type of strobilation by scyphistomae because gastrovascular structure is an attribute only of individuals that cannot contribute directly to the numerical magnitude of a bloom. Yet differences in canal structure are correlated with the ability to aggregate, bloom, and swarm (Figs. 1, 2, 4). Primarily taxa with extensive canal systems occur *en masse* whereas those without usually do not. We hypothesize the circulatory system is one of the most important anatomical features enabling bloom formation because it allows individual medusae to grow to large size. Large size enables attributes that promote occurrence *en masse*: increased feeding, increased fecundity, and natatory movement against the predominant flow.

### *Size*

Jellyfish blooms are characterized by rapid, seemingly sudden, increase in abundance of medusae. Blooms are therefore necessarily initiated by production of large numbers of ephyrae, and blooms are typically thought of in terms of rapid increases in numerical abundance. However, numerical abundance alone is demonstrably insufficient to constitute a bloom. First, blooms that draw attention are never of ephyrae although, assuming remotely normal life-tables, most ephyrae must die before developing into medusae, so the problematic true blooms of scyphomedusae that are reported must comprise a reduced number of individuals. Second, blooms of hydromedusae, which are almost exclusively small, are rare (see Hamner & Dawson, 2008). The principal exceptions are *Aequorea* (e.g., Purcell, 1989), which is the largest hydrozoan, and introduced species such as *Craspedacusta* landlocked in freshwater lakes (Pennak, 1956) and *Moerisia lyonsi* in Chesapeake Bay (e.g., Purcell et al., 1999). Thus, the aspect of true blooms that makes them remarkable is the rapid growth of the individual medusae that survive, which produces a remarkable increase in population biomass. The mass of mature scyphomedusae is thousands to hundreds of thousands of times greater than the mass of ephyrae, an increase that can be achieved through growth in just a few weeks to few months but which would take many orders of magnitude greater duration to achieve through strobilation. Thus, using food to promote somatic growth may increase population biomass much faster than increasing the number of juveniles of small size (Alldredge, 1984; Arai, 1997).

### *Growth rate, feeding rate*

The rapid growth of semaeostome and rhizostome scyphomedusae is enabled in two ways: (1) by construction of mesoglea to achieve large increase in size at relatively low metabolic cost and (2) by use of their large external surface as their primary feeding structure. Because scyphomedusae are diploblastic (but see Seipel & Schmid, 2006), ingested materials are allocated to increasing the 2-dimensional surface areas of the endoderm and ectoderm rather than, as in many 'higher' metazoans, fueling a disproportionately metabolically demanding 3-dimensional mesoderm. Increasing the third dimension—depth and thus body volume—in jellyfish is effected primarily by construction of mesoglea composed almost entirely of highly dispersed collagen molecules with exceptionally low metabolic requirements (Chapman, 1966; for other functions of mesoglea see e.g., deBeer & Huxley, 1924; Denton & Shaw, 1962; Chapman, 1966; Hamner & Jenssen, 1974; Thuesen et al., 2005). Exponential growth in biomass is thus possible, as documented in linear rates of bell diameter increase (e.g., Arai, 1997: Figs. 7.2, 7.3) and therefore cubic increases in volume in *Aurelia*.

The rate of growth of medusae via deposition of mesoglea is impressive not only in terms of its efficient allocation of resources (although estimates of conversion efficiency in medusae vary greatly from 2% to 37%; Arai, 1997, p. 185) but also in its effect on acquisition of new resources. Many semaeostome and all rhizostome scyphomedusae use a significant portion of their large external surface as their primary structure for prey capture; shallow-water cyaneids and ulmarids have extensive tentaculate surfaces while rhizostomes possess oral arms covered in suctorial mouths. When these medusae invest resources in exponential growth of their surface area, therefore, they also allocate those resources for exponential increase of their feeding potential. Individual feeding success of *Aurelia* therefore increases proportional to the area of the bell (Martin, 1999, p. 54) and exponentially with diameter (e.g., Bailey & Batty, 1983; de Lafontaine & Leggett, 1987). This in turn underwrites a rapid, non-linear, increase in prey capture (Arai, 1997,

Table 3.5) and, further, exponentially increased allocation to growth. We note this may not be the case for medusae that are photosymbiotic (e.g., García & Durbin, 1993) or others such as box jellyfishes, coronates, and pelagiids or deepwater cyaneids, which 'fish' for prey with few long tentacles, but expect that many other scyphomedusae may grow exponentially, given sufficient food, until they reallocate resources from growth to reproduction.

*Fecundity*

At maturation, the energy supporting exponential increase in body mass and feeding capacity is redirected into production of eggs and/or sperm, generating a rapid volumetric increase in reproductive capacity. A doubling of bell diameter in *Rhopilema esculenta* (Kishinouye) results in a 20-fold increase in daily egg production (Huang et al., 1985), and the number of eggs and larvae brooded by *Aurelia* increases linearly with the wet-weight of the medusa (Schneider, 1988). Large size thus greatly increases reproductive output of individuals and large individuals should, therefore, have a fitness advantage in terms of reproductive success. This selective benefit is one instance of a more general phenomenon known as "fecundity advantage" (Shine, 1988, 1989) first proposed by Charles Darwin (1874, p. 332) as a mechanism for maintaining larger female than male size and probably best known as an explanation for protandric hermaphroditism. Fecundity advantage has garnered considerable, but not unanimous, support (Shine, 1988) from studies of diverse organisms including copepods, cladocera, and rotifers (Gilbert & Williamson, 1983) but to our knowledge has not previously been tested in scyphomedusae. (N.B. Reanalysis of data describing bell diameters of *Aurelia* caught in net hauls on 13 occasions between September 1995 and December 1998 in a marine lake, Palau, reveals the largest medusae were usually female [$\chi^2 = 4.76$, d.f. $= 1$, $P < 0.0145$ one-tailed]. Female *Aurelia aurita* (Linné) are also larger than contemporaneous male *A. aurita* in Horsea Lake, England (see Lucas & Lawes, 1998, Figs. 2, 5), and female *Catostylus mosaicus* (Quoy & Gaimard) are predominantly larger than contemporaneous males in Botany Bay, New South Wales, Australia (Pitt & Kingsford, 2000, Fig. 3B). Thus, it is clear that the pulsed life-history style of scyphozoans has potential to create large populations of planulae and tiny scyphistomae, which can reproduce asexually *en masse* to provide the raw material—numbers of individuals—of which the growth could turn into the biomass of the next year's bloom.

*Natation, Reynolds number*

In addition to the life-history factors discussed above, the fact that small medusae may occur in large numbers but, unlike large medusae, apparently rarely form exceptional blooms ('population explosions' or 'booms') and do not swarm (but see Hamner & Dawson (2008) for some apparent exceptions) is in part a function of their ability to actively aggregate despite environmental factors that serve to diffuse them. Whether medusae have the potential to aggregate despite their immediate fluid environment depends upon their tendency to move forward, i.e., inertia, generally exceeding viscous forces retarding them, a relationship summarized by the Reynolds number.

Reynolds number describes how fluid density ($\rho$) and dynamic viscosity ($\mu$) interact with an organism's morphology (size and shape, but particularly length in the direction of flow, $l$) and speed ($U$), as follows: $Re = \rho * l * U * 1/\mu$. If $Re$ approaches unity or less, drag forces dominate and bring medusae to an abrupt halt at the end of each power stroke, as evident in videos of the saltational movement of ephyrae just liberated from strobilae and the movement of small prolate hydromedusae such as *Proboscidactyla flavicirrata* Brandt or small oblate hydromedusae such as *Mitrocoma cellularia* (A. Agassiz) (e.g., Colin & Costello, 2002). If $Re >> 1$, the organism's momentum dominates and it continues to glide with no discernible deceleration between power-strokes, as is the case for the large scyphomedusa *Stomolophus meleagris* L. Agassiz (Arai, 1997, p. 51). It is apparent from the equation that the characteristic length of medusae, which may vary three orders of magnitude, from a few millimeters to over 1 m, is the principal factor influencing a medusa's movement; speed varies by only one order of magnitude, and fluid density and dynamic viscosity of seawater are to all intents and purposes constant. Thus, an ephyra swimming at less than 1 cm $s^{-1}$ has $Re \approx 25$, a small *Pelagia* swimming at 2 cm $s^{-1}$ has $Re \approx 600$, a medium-sized rhizostome such as *Mastigias* swimming at 8 cm $s^{-1}$

has $Re \approx 2{,}000$, and a large rhizostome such as *Rhizostoma pulmo* (Macri) moving at 15 cm $s^{-1}$ has $Re \approx 100{,}000$ (estimates based on information from Aleyev, 1977; Arai, 1997; Dawson & Hamner, 2003, 2008).

Aleyev (1977), in addition to calculating organisms' *Re*, also classified swimming organisms in terms of their ratio of frontal diameter (*d*)/characteristic length (*l*). Aleyev's *d/l* is the inverse of 'fineness,' which is more commonly used in studies of the mechanics of jellyfish swimming (e.g., Costello & Colin, 1995; Colin & Costello, 2002; Dabiri et al., 2007). However, *d/l* is somewhat more holistic because it is affected by the form of oral arms and other appendages that trail the bell, whereas 'fineness' is typically calculated only for the bell of medusae that have no, or few, pendant oral structures (e.g., Colin & Costello, 2002). According to Aleyev's (1977) scheme, organisms with $Re < \sim 10^4$, irrespective of their *d/l*, and organisms with $Re < \sim 10^5$ and $d/l > 0.4$ are euplankton. Organisms with $10^4 < Re < 10^5$ and $d/l < 0.4$ are planktonekton. Organisms with $10^5 < Re < 10^7$ and $d/l < 0.4$ are nektoplankton. It is clear that, according to these generic descriptions, most scyphomedusae are euplankton, but that some semaeostomes and a considerable proportion of large rhizostomes, the principal clades of blooming and swarming species, are planktonekton or nektoplankton and thus have reasonable ability to determine their local position. For example, *Chrysaora* in Monterey Bay can swim directionally with astonishing accuracy even at night (Morris, 2006), presumably facilitating population maintenance (Sinclair, 1988). *Stomolophus meleagris* can navigate along continental shelves (Shanks & Graham, 1987), possibly using shear forces to orient, as is the case in *Aurelia* (Rakow & Graham, 2006).

It is important to note that these broad classifications only suggest tendencies because local hydrographic conditions may interact with medusa morphology in important ways. For example, in Saanich Inlet (Vancouver Island, British Columbia), during Spring, *Aurelia labiata* Chamisso & Eysenhardt ephyrae and small medusae are dispersed by tidal currents throughout the fjord because they are too small and too slow to avoid dispersal by ambient flow (Hamner et al., 1994). Yet when the jellyfish grow to bell diameters of about 4–6 cm they can make headway against reduced tidal currents within the fjord, and they swim directionally and horizontally toward the south-east during daylight hours using a time-compensated sun-compass navigation system, often swimming hundreds of meters to the south-east each day; bigger medusae migrate faster, and all accumulate eventually into small coves on the south-east side of Saanich Inlet in late summer (Hamner et al., 1994). Once in the embayments the jellyfish maintain their geographic position by changing their behavior, swimming vertically instead of horizontally during the day as well as at night. Tidal currents do not advect the jellyfish away because tidal currents tend to shear across the mouths of the coves. Thus, medusae accumulate, begin to spawn in late summer, and these specific behaviors are thus apparently adaptations that maintain the population within the specific physical context of Saanich Inlet. To the north, in Roscoe Bay, British Columbia, *Aurelia labiata* behave quite differently, swimming predominantly westward during sunny afternoons (Albert, 2005, 2007, 2008).

It is possible that passive dispersal of tiny ephyrae and small juveniles followed by active reaggregation by sexually maturing medium-to-large medusae is a common theme in the larger scyphomedusae. If true, this process likely has many facets, being aided by rhopalia, circadian rhythms, neural processing for a time-adjusted sun compass, and ontogenetic change in swimming ability perhaps attributable to changes in musculature and oral arm form.

## Form of oral arms and tentacles

The oral arms and tentacles have evolved dramatically within Scyphozoa, particularly Discomedusae. These modifications likely have an important influence on flow regimes, feeding potential (or 'clearance rate'), and prey type ('selectivity').

Coronates all have oral appendages that are limited to simple lips on a short manubrium and, with few exceptions, an array of robust aborally arcing marginal tentacles. In the case of *Atolla*, the marginal tentacles are complimented by a remarkable trailing hypertrophied tentacle (Larson, 1979; Hunt & Lindsay, 1998). Few in situ observations are available, but it is likely that the mesopelagic coronates use the aborally arcing marginal tentacles to capture zooplankton including small crustaceans and fishes (Larson, 1979) supplemented in *Atolla* by use of the

hypertrophied tentacle to capture gelatinous zooplankton such as the physonect hydrozoan *Nanomia* (Hunt & Lindsay, 1998). While shallow-water tropical *Nausithoe* also have aborally arcing marginal tentacles and a predatory diet (Colin et al., 2006), these tentacles are greatly reduced in the epipelagic photosymbiotic *Linuche* (Mayer, 1910, plate 59).

The basal pelagiid semaeostomes, like coronates, possess 8 to 40 long ribbon- or thread-like nematocyst-bearing contractile feeding tentacles, but unlike coronates, these are all trailing and supplemented by four highly convoluted oral arms (Gershwin & Collins, 2002). Other semaeostomes, depending on their family and habitat, have few thick ribbon-like tentacles and flouncy oral arms (deepwater cyaneids *Desmonema* and *Drymonema*), curtains of fine thread-like tentacles supplemented by extravagant draping oral arms (shallow-water *Cyanea*, *Phacellophora*), many fine tentacles and digitate oral arms (Aureliinae), or large oral arms and no tentacles (deepwater ulmarids). This morphological variation is matched by, and likely causes, differences in diet among these medusae. Pelagiids capture relatively few but relatively large active zooplankton prey such as euphausiids and also juvenile fish with its ribbon like tentacles; *Chrysaora fuscescens* Brandt occasionally captures and eats juvenile *Loligo opalescens* Berry in Monterey Bay (Hamner pers. observations). They may also catch microzooplankton on their oral arms. The cyaneids and *Phacellophora* may capture large numbers of gelatinous zooplanktonic prey, engulfing them in their curtain-like oral arms. In contrast, the neritic ulmarid *Aurelia* relies almost solely on its curtain of fine tentacles to capture micro- and mesozooplankton, its oral arms being used to transport boluses of food from the oral margin to the central mouth.

These observations suggest an evolutionary trend within Scyphozoa and Semaeostomeae from capturing large prey items through contact-fishing to feeding on smaller prey captured using a fine filtration-type apparatus. Interestingly, though, food handling in all species involves extra-gastric digestion of captured prey, thus speeding passage through the gastrovascular cavity. Gelatinous prey, fish, or squid too large to ingest are digested and/or reduced in volume outside the stomach within the foliose oral arms of pelagiids and cyaneids (Strand & Hamner, 1988; Arai, 1997, p. 96; Hansson, 1997).

Rhizostome medusae, with no marginal tentacles, continue the trend of increasing specialization on more numerous smaller prey but evolved a quite different morphological solution for exploiting small prey. Rhizostomes have eight oral arms, pendant behind the bell, over which water is forced during swimming (e.g., D'Ambra et al., 2001). These large highly reticulated external feeding surfaces have myriads of tiny suctorial mouths with which they filter and capture very many meso- and microzooplankton prey (e.g., D'Ambra et al., 2001; Peach & Pitt, 2005). The form of the oral arms, sometimes with appendages, creates a prolate morphology, with longer characteristic length ($l$) relative to diameter ($d$) compared to the generally oblate morphology of, for example, *Aurelia*, with a potentially large effect on their swimming ability and feeding. Large prolate medusae must have much larger *Re*, faster swimming speeds, and more consistent swimming motion, than oblate medusae of similar bell diameter, indicating they should be able to capture more, smaller, faster prey (D'Ambra et al., 2001). This simple hypothesis, though, belies greater complexity because the dimensions and presentations of oral arms show considerable variation, including the flat spray of *Cassiopea*, the relatively squat oral arms of *Cephea* and *Mastigias* which in the latter case are appended by long mouthless terminal clubs, and the long coursing oral arms of *Thysanostoma*. These different morphologies suggest multiple functions of the oral arms, not restricted to prey capture alone, such as increasing surface area for photosymbiosis in many Kolpophorae or increasing swimming efficiency via streamlining or hydrodynamic stabilization in natatory medusae such as *Mastigias* (including the terminal clubs; see, e.g., Dawson & Hamner, 2003), *Thysanostoma*, and possibly other fast-swimming species (e.g., Catostylidae).

## Photosymbiosis, lack of photosymbiosis

Photosymbiosis between Scyphozoa and dinoflagellate zooxanthellae has evolved at least three times (Fig. 3B). Notably, none of the photosymbiotic medusae—*Cassiopea*, *Mastigias*, *Rhizostoma*, *Linuche*, *Cephea*, *Cotylorhiza*, *Catostylus*, and *Phyllorhiza*—form blooms, with one remarkable exception: invasive, aposymbiotic *Phyllorhiza* in the Gulf of Mexico (Bolton & Graham, 2004). In

contrast, the azooxanthellate *Aurelia*, *Pelagia*, *Catostylus*, *Cephea*, *Crambionella*, *Nemopilema*, and *Rhopilema* (and the large azooxanthellate hydrozoan *Aequorea*) all aggregate and bloom.

This suggests that the exploitation of two quite different sources of energy, or the potentially more constant supply of energy available to photosymbionts (Arai, 1997, p. 114), may diminish the tendency of jellyfish populations to bloom. Trophic generalism achieved through exploitation of a broad resource base or resource switching may insure a predator population against large fluctuations in one or another target prey (Hanski et al., 1991; Ricklefs & Miller, 1999, pp. 450, 461; Behmer & Joern, 2008) allowing the predator to achieve a temporally more even, or 'balanced,' energetic income. However, the dynamics of even seemingly facile one-consumer-two-resource systems can be complex and may not lead to relatively stable, moderate density, predator population sizes (e.g., Bonsall & Hassell, 1997; Kooi et al., 2004; Ives et al., 2008). Despite some evidence that cnidarian's symbiont genotypes may be 'shuffled' to suit different circumstances (Baker, 2003), others have argued that this is a rare ability (Goulet, 2006) and there is evidence that host dependencies on symbiont and prey cannot be switched (Tanner, 2002). Furthermore, predator–prey dynamics may proceed to extreme abundances due to temporal environmental variation, spatial heterogeneity, and dispersal (e.g., Gotelli, 2001) and while symbiotic cnidarian populations are well known to 'bust' (or 'crash') during bleaching events under extreme environmental conditions (e.g., Dawson et al., 2001), we have not found evidence that photosymbiotic scyphomedusae 'boom.'

An alternative explanation for the lack of blooms of photosymbiotic scyphomedusae, perhaps more robust than relying on a seemingly precarious balance between symbionts, might instead draw on evidence that symbioses involve trade-offs for both host and symbiont. This would be more in keeping with the implications of the adaptive bleaching hypothesis (Fautin & Buddemeier, 2004) and with theory that suggests symbioses are, in general, slightly maladaptive (e.g., Thompson et al., 2002). Thus, although high availability of specific food types could be inferred as an important potential environmental cause of blooms, we instead hypothesize that the more important facet influencing whether a species can bloom is its inherent ability to exploit available food. Photosymbiosis might limit the ability of host medusae to assimilate abundant prey through perhaps physiological mechanisms (for which we propose invasive *Phyllorhiza* as a model), or via trade-offs against particulate food capture (Arai, 1997, p. 116). Other hypotheses for the dearth of blooms of photosymbiotic scyphomedusae might include other limiting factors of the symbiosis, such as the availability of zooxanthellae to inoculate new polyps that require the symbiosis for strobilation (e.g., Sugiura, 1964).

## Habitats potentially related to accumulation

Only shallow water medusae occur *en masse* (Fig. 3D), often in habitats broadly distributed geographically, and with no phylogenetic bias beyond that which exists due to other ecological, life-history, or anatomical reasons (e.g., Figs. 2, 3A, B, 4). Shallow-water *Aequorea* bloom, the coronate *Linuche* resists dispersion between times when Langmuir cells force it to aggregate (Larson, 1992), and many semaeostomes and non-photosymbiotic rhizostomes include species that form blooms. In contrast, deepwater coronates and deepwater semaeostomes, also often distributed widely, do not bloom. As described by Omori & Nakano (2001), for commercially fished species, the "places where great numbers of…jellyfish occur are characterized by having a large tidal range, shallow depth, semi-enclosed water mass, freshwater inflow through river systems and development of mangrove swamps. Such factors apparently create favorable conditions for settling of polyps and recruitment." These factors or their analogues (e.g., non-mangrove shallow-water habitats in Europe and North America), or their correlates, may still be favorable for jellyfish even if all do not occur together. Yet, for the most part, the effects of these environmental variables and the mechanisms by which they might increase jellyfish abundance remain to be quantified (but see, e.g., Hofmann & Crow, 2002).

Strong seasonality, whether temperate or monsoonal, seems likely to be the ultimate source of favorable, and unfavorable, conditions which provide resources for successful growth and reproduction during only a fraction of each year. This has the potential to compress life cycles, and thus life-history

stages, into relatively discrete periods which enforce coordinated cohorts. Such environmental forcing is expected to affect the scyphozoan populations and also their prey. Unusually successful cohorts, i.e., population explosions or 'booms,' may therefore be explained by Hjort's "critical stage" (Ottersen & Loeng, 2000; Hjort, 1914; cited in Stenseth et al., 2002) or Cushing's (1975, 1983, 1984) "match/mismatch" hypotheses, wherein large cohorts of predators result when peaks in feeding larval stages coincide with abundant resources; annual blooms would result from good matches, and 'crashes' or 'busts' from mismatches.

Seasonal abundance may also be exaggerated over interannual timescales by the predominant 'color' of variation in coastal environments. Environmental variance in marine environments commonly occurs as 'red noise,' i.e., consecutive measurements made on short time scales, commonly perceived as 'ecological' timescales (although these are also microevolutionary timescales), are autocorrelated. Autocorrelation can lead to multiannual periods of 'good years' or 'bad years,' a pattern that is expected to lead to population 'booms' (or unusual 'blooms') and population 'busts' (Lawton, 1988; Cuddington & Yodzis, 1999; Brodeur et al., 2002) depending on the organisms' abilities to respond to such fluctuations. This is not the case for deepwater habitats, in which the magnitude of variation is less than that in shallow-water coastal environments.

## Summary of patterns

Mass occurrences of jellyfish involve a phylogenetic subset of Medusozoa. The current analyses of higher taxa are limited by small sample size and incomplete information for almost all taxa, therefore we do not attempt detailed statistical analyses which would have no power to establish phenotype-environment correlations. Rather, our six preliminary conclusions (below) represent hypotheses requiring further research at the species and genus levels that may allow identification of causal versus coincidental correlations. Some of these may not be independent of each other, but rather may positively feedback increasing the potential of certain species to aggregate, bloom, or swarm.

### 1. Character complexes

Multiple organismal traits contribute to the formation of aggregations, blooms, and swarms. Many of these traits appear to co-occur when their evolution is traced on the medusozoan tree of life, occasionally originating together independently in Hydrozoa and Scyphozoa. Subsets of these traits likely form 'complexes' of characters that cannot be separated functionally and are not evolutionarily independent. These include many anatomical attributes associated with large size, behavioral attributes of large size, and morphological traits affecting prey capture.

### 2. Phenotype-environment correlates

Multiple components of phenotype and environment must interact to cause mass occurrences of scyphomedusae. No single factor alone is sufficient because no species, nowhere, blooms all the time (to our knowledge). The deepwater ulmarids, for example, are large enough to be probably nektoplankton or planktonekton and have highly reticulated canal systems to distribute nutriment, yet they do not form blooms—possibly because of attributes associated with life in the deep sea including low fecundity, direct development, slow growth, a relatively stable environment, and perhaps few cues to promote aggregation. The kolpoform rhizostomes, which have many anatomical and distributional commonalities with the daktylioform rhisozostomes, do not bloom possibly because they are photosymbiotic. *Pelagia* may be the best bloomer in Pelagiidae because the canal pouch may be relatively efficient for medusae of its relatively small size, but not for many of the larger *Chrysaora* species. Probably the best-known examples of the multifaceted nature of mass occurrences are the many documented cases of aggregations resulting from the interaction of intrinsic behavior and the local hydrographic environment (e.g., Hamner et al., 1994; Graham et al., 2001; Rakow & Graham, 2006).

### 3. Asexual reproduction by polyps increases the potential for blooms of medusae

Podocyst formation, strobilation, and potentially other modes of asexual reproduction by polyps can

greatly increase the potential size of any subsequent medusa population. Such potential is generated in the form of small life-history stages that generally go unnoticed and/or have little ecological impact thus emphasizing, by stark contrast, the apparent effect when medusae occur *en masse*. In particular, polydisc strobilation is associated with swarming. For example, *Aurelia* and Daktyliophorae engage in polydisc strobilation and are often blooming species; Kolpophorae do not engage in polydisc strobilation and are not blooming species (confoundingly, they are also photosymbiotic).

4. Large size is the principal organismal attribute leading to blooms and swarms

Small jellyfish (e.g., hydromedusae except *Aequorea*), or small life-history stages, cannot form blooms or swarms, except under exceptional circumstances, irrespective of whether they have other attributes that could promote occurrence *en masse*. Large size is important for medusae to

a. *overcome fluid dynamic constraints* and swim strongly enough to reaggregate behaviorally,
b. *have capacity to consume prey items with such rapidity that population biomass can increase exponentially* such that prey populations can be depleted and the medusa population will
c. *become hyper-fecund*, potentially increasing population size of small polyps dramatically.

5. Feeding strategy can enable or inhibit bloom formation

Jellyfish blooms are favored if medusae have feeding morphologies that enable them to take advantage of rapid increases and high abundances of prey and that, conversely, limit population size when target prey abundance is low. Thus, blooms are most likely to occur in species that

a. *are not photosymbiotic*, because zooxanthellae may physiologically constrain the host's ability to take advantage of rapid increases in prey availability, and
b. *specialize on lower trophic levels*, such as microzooplankton, in which energy is more abundant, more easily renewed, and more likely to have large variations in availability.

6. Habitat can enable or inhibit aggregation, bloom, or swarm formation

Local environmental conditions may ultimately govern whether a population of a particular species can bloom or not. For example, coastal environments provide pulsed seasonal resources and large amounts of habitat for benthic polyp stages; many embayments provide more placid hydrodynamic regimes in which even medium-sized prolate medusae may be able to aggregate behaviorally. There are insufficient resources in the deep sea to support the huge biomass associated with surface swarms, but long-lived *Periphylla periphylla* Péron & Lesueur can accumulate in Scandinavian fjords because medusae are not advected away and because food is more plentiful than in the deep sea.

## Synthesis and caveat

Jellyfish that aggregate, bloom, or swarm are clustered taxonomically and phylogenetically; the taxa that include blooming and swarming species are usually more diverse than their non-accumulating sister taxa (Hamner & Dawson, 2008). We have shown here that possession of a suite of life-history and phenotypic traits—podocysts, strobilation (particularly polydisc strobilation), ephyrae, circular and radial canals, large size, high fecundity, oral arms modified for suctorial feeding, fine filtering tentacles, high feeding capacity, lack of photosymbiosis, rapid growth—appears phylogenetically correlated with the species-rich clades that bloom or swarm. From a functional perspective, there is reason to expect that these traits confer the ability to occur *en masse* and some related evolutionary benefit (i.e., diversification). We have also outlined environmental situations—protected shallow-water coastal habitats—that most often facilitate or promote mass occurrences of jellyfishes (see also Omori & Nakano, 2001). Consequently, because mass occurrences of jellyfish that have occurred are largely explainable, we hypothesize that those yet to occur should be

mostly predictable, assuming relatively consistent phenotype-environment interactions.

Unfortunately, our list of phenotype-environment correlations currently must be incomplete and somewhat poorly bounded due to the spatially and temporally haphazard historical record of accumulations (and their absences), phylogenetically incomplete sampling, and descriptions of species of medusae still lacking morphological, ecological, and physiological details. Our analyses therefore serve to constrain, rather than define, the suites of characters and conditions that favor jellyfish blooms. With that admonition in hand, we believe that the suites of permissive characters remain informative and intriguing and that the tools of evolutionary biology can provide novel insight into the occurrence of jellyfish blooms and swarms.

## Adaptive accumulations, changing circumstances, and exaptive excesses?

Important transitions in the evolution of jellyfish accumulations—from aggregations to blooms and swarms—coincide with the evolution of select life-history and morphological characters. These characters are, by way of correlation, inferred to have enabled blooming and swarming and are, because of the evolutionary success of the clades in which they occur, inferred to be adaptive, either individually or in concert. Are blooms also adaptive? That is, are blooms and swarms themselves adaptions, as opposed to simply the sum of their component parts? And are recent unusual or unnatural blooms adaptive, or perhaps exaptive?

Many medusozoans differ from most other marine animals (e.g., species of bivalves, sea urchins, reef fishes) because the large sexually reproducing stage, rather than the tiny larval stage, has long pelagic duration. The larval and subsequent early developmental stages are mostly benthic in cubozoans and scyphozoans but mostly pelagic in other non-brooding invertebrates and vertebrates. Thus, although the cubozoans, scyphozoans, marine invertebrate broadcast spawners, and many reef fishes liberate massive numbers of very tiny individuals (cubomedusae, ephyrae, or larvae) into the water column, their life-history strategies subsequently diverge. The cubozoans grow and ephyrae metamorphose into planktonic juvenile medusae which remain in the water column through reproduction and senescence; in contrast, the larvae of other taxa metamorphose into late-stage larvae or juveniles and settle quickly into benthic communities. These two groups of tiny plankton thus have different selective forces to navigate if they are to meet demographic and evolutionary metrics of success, i.e., contributing offspring with their alleles to the next generation. The problem for medusae is to stay with their conspecifics, oftentimes near the location in which they were spawned, whereas the problem for other larvae is to find conspecifics in distant places despite the diluting effect of oceanic long-distance dispersal. While both may benefit from some kind of gregarious behavior, which has been demonstrated abundantly in planktonic dispersers such as barnacles, oysters, and tubeworms (Toonen & Pawlik, 2001; Dreanno et al., 2006; Tamburri et al., 2007) but for which there is still no convincing evidence of full or half sibs settling together distant from the parental location (Veliz et al., 2006), it is clear that medusae would not require gregariousness *per se* if they shared an appropriate suite of favorable life-history and behavioral traits. If all medusae in a demographic population started their planktonic life as ephyrae in the same approximate location at the same approximate time, a suite of shared responses to local environmental stimuli could lead, without any intervening interaction between individuals, a reasonable proportion of the population to still be in relatively close proximity at maturation. That said, a plausible mechanism is still required through which natural selection could maintain coordinated life histories and behaviors. While traits that enable medusae to originate in a short period of time, avoid advection away from the population (excepting those fortunate enough to be advected to another population elsewhere), avoid predation, and find and capture and consume food, all have proximate causes and immediate benefits to the individual (e.g., temporal 'matching' with food supply, retention in areas proven favorable for parents [not necessarily medusae in the preceding year]), they can never sum to more than growth and survival of individuals if the medusae do not subsequently encounter mates and reproduce sexually. In contrast, the medusae that do find mates can reproduce, pass on alleles that enhance mass occurrence, and have offspring that are 'fitter' than average and which in turn are also more likely to

reproduce. Thus, we hypothesize that blooming and swarming are key adaptations that exert strong selective pressure and secure together the many component traits into one complex adaptation.

The evolution of aggregation, blooming, and swarming is thus apparently an emergent property subsequently favored by natural selection, a 'key innovation' (Donoghue, 2005). The many component traits were already adaptations in their own right for, say, increased feeding potential, increased fecundity, avoidance of advection, etc., before they also became exaptations for mass occurrence resulting from selection for breeding accumulations. An unusual example may illustrate this point. In Palau, *Mastigias* medusae in ancestral lagoonal populations and derived lake populations exhibit diel horizontal migrations that result in accumulations in all locations during the early morning and late afternoon. These accumulations could be reproductive swarms, but in fact result from selection for patterns of migration that maximize exposure of their photosymbionts to sunlight or minimize deaths caused by predatory anemones (Hamner & Hauri, 1981; Dawson & Hamner, 2003). The evolution of these accumulations is therefore not selection for reproduction, but a consequence of accumulation may be increased reproductive success.

Therefore, it is possible that for semaeostomes the evolutionarily basal and predominantly open coastal and oceanic pelagiids may occur *en masse* through a different balance of mechanisms under different selective pressures than those favoring mass occurrence of medusae such as *Aurelia* in semi-enclosed coastal environments. For example, *Chrysaora* can occur at high densities (16 $m^{-3}$) in narrow salinity and temperature regimes in the Chesapeake Bay (Decker et al., 2007) but are typically more disperse in open coastal environments (e.g., 1 to 100 per 10,000 $m^{-2}$, Doyle et al., 2007; also K. Bayha, pers. comm.), so *Chrysaora* may aggregate in suitable habitat in highly structured coastal waters (a pattern exaggerated by death if advected into neighboring unsuitable habitat), or bloom in coastal waters due to high rates of strobilation and dense or expansive polyp fields, but in neither case truly swarm. Similarly, *Pelagia* in the open ocean among West Papua's islands were observed over a spatial extent of at least 40 km on several different occasions spanning several weeks, but never in densities of more than a few individuals per cubic meter except where they were concentrated by local topography (M. Ammer, M. Dawson, B. Hoeksema, L. Martin, pers. obs.).

Thus, although we identified three classes of mass occurrence—aggregation, blooming, and swarming—at the beginning or our analyses (Hamner & Dawson, 2008), we recognize that these may be artificially discrete classifications of a character complex whose states are continuously distributed. Coarsely similar accumulations could result from convergence of different evolutionary pathways (see discussion in Donoghue, 2005), which should be apparent from detailed analyses of factors contributing to particular mass occurrences. Thus phylogenetic analyses of adaptations, exaptations, and key innovations require nuanced analyses of rich datasets that consider changes that accumulate across a nested series of nodes in the evolutionary tree (Donoghue, 2005). The first step toward this goal is a more explicit empirical approach to describing factors influencing, or potentially influencing, jellyfish accumulations, including places of origin, places of occurrence, physical environment, and life history. Also needed are more explicit descriptions of blooms themselves in terms of number and biomass, perhaps based on rates of increase relative to initial conditions and long-term population dynamics. This will not only enable more robust phylogenetic macroevolutionary analyses, but also improve microevolutionary studies of mass accumulations through detailed comparisons of potentially closely related populations (e.g., Hamner et al., 1994; Lucas, 2001; Albert, 2005, 2007, 2008).

Our inferences suggest an evolutionary explanation for why "species that have always been present suddenly experience severe increases or 'blooms', often with little evidence of what caused the population increase" (Mills, 2001). Simply, they have sufficient requisite exaptations for blooming such that, when environmental circumstances change to promote blooms, they are able to take advantage of the new conditions. Thus, over-fishing and eutrophication, which may lead to increases of microzooplankton populations, can cascade into jellyfish blooms; introduced species that can compete well for or exploit poorly used but abundant resources in the invaded location have increased potential to bloom; changed environmental conditions due to global warming, such as altered phenology or hydrography, may make new

resources available or enable aggregations in new places and times.

The applied question that interests us is whether such changes will predictably lead to blooms. The predictions that attract most attention generally project oceans dominated by jellyfish (e.g., Dybas, 2002; http://www.shiftingbaselines.org/videos/index.html). However, as described by Mills (2001) and Purcell (2005), and as evident in our analyses, the answer to this question depends on the species, environment, and changes concerned. For example, if the local environment changes so that food availability is increased and relatively strongly pulsed in spring—for example, through increased rainfall, run-off, and nutrient enrichment—then we expect this to provide the opportunity for blooms to form. But, blooms will only form if there is a jellyfish species present that has the morphological and behavioral characteristics that enable it to take advantage of those resources such that many small ephyrae can grow rapidly to large size. In a reasonable proportion of cases, we can expect phenological changes to disfavor populations that already exploit pulsed resources. Hjort's (1914) first feeding and Cushing's (1975, 1983, 1984) match/mismatch hypotheses, wherein large cohorts of predators result when peaks in predator and prey populations coincide, cut both ways in times of environmental change.

## Closing remark

An important point worth emphasis is that our discussion so far has focused on the ecological responses of jellyfish to environmental change due to previously evolved characteristics. Yet many jellyfish species likely have considerable diversity within the very large populations of which they are comprised and therefore should have considerable potential for evolution when stabilizing selection is disrupted or redirected. Consequently, it is also important to consider what future evolutionary consequences may be caused by environmental change. We currently have no knowledge of the strength of selection on any traits, or of how the strength or direction of selection may be altered by changed conditions. Consequently, we believe that descriptive research must be complimented by experimentation, including the standard tools of evolutionary ecology and ecological genetics such as reciprocal transplants (when ethically appropriate), 'common garden' experiments, and field-based or laboratory-based manipulations. Such experiments may be guided by the many models of climate change now available that describe possible ranges, and likely trajectories, of environmental perturbations, at least on regional scales although local changes may vary.

Some data are available in the literature, and abundant data are collectable from nature, that could be used to corroborate laboratory (or field) experiments. Unfortunately, these data are often sporadic, as illustrated by our review (Hamner & Dawson, 2008), and for most taxa most data simply are not yet available. A global perspective on jellyfish ecology and evolution, of the kind only achievable through concerted coordinated effort, is required to rapidly reduce deficits in our knowledge of and ability to explain jellyfish blooms (and aggregations and swarms). Initiatives for regional and global programs focusing on the ecology of diverse scyphozoan taxa, identified accurately and placed phylogenetically, seem an essential next step to meet current needs for increased understanding of the past and future evolution of jellyfish blooms.

**Acknowledgments** Detailed critiques by M. Arai, P. Hamner, L. Martin, K. Pitt, J. Purcell, H. Swift, and two anonymous reviewers, and discussion with K. Bayha, L. Gomez Daglio, J. Lehman, and J. Vo helped improve and organize the content and presentation of this manuscript. WMH thanks the organizers of the 2nd International Jellyfish Blooms Symposium, K. Pitt and J. Seymour, for the invitation to present a plenary address at the meeting, and we thank the Editors for their patience and industry in preparing this volume. Allen G. Collins kindly provided the datamatrix for analyses in Fig. 2. This work was supported in part by grant DEB-0717078 from the US National Science Foundation to MND and AGC.

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